The first fossil record of the Sawshark Pliotrema (Pristiophoridae) from the Neogene of the South-East Pacific (Chile)

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THE FIRST FOSSIL RECORD OF THE SAWSHARK *PLIOTREMA* (PRISTIOPHORIDAE) FROM THE NEOGENE OF THE SOUTH-EASTERN PACIFIC (CHILE)

PRIMER REGISTRO FÓSIL DEL TIBURÓN SIERRA *PLIOTREMA* (PRISTIOPHORIDAE) DEL NEÓGENO DEL PACÍFICO SUDESTE (CHILE)

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Short Description: Paleobiogeographic and paleoecological implications of a fossil specimen of Pliotrema from the eastern Pacific of South America

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Abstract. We present the first fossil record of the sawshark genus *Pliotrema* from the south-eastern Pacific Ocean. The examined material was obtained from a little-known fossil locality named "Arenas de Caldera" in the Atacama region of Chile. The fossiliferous deposits belong to the Bahía Inglesa Formation, which is most likely of middle Miocene-early Pliocene age. There are no extant species of this sawfish in the eastern Pacific, probably due to the onset of cooling conditions during the Neogene. The type of environment for the elasmobranchs reported in this study is interpreted as demersal, based on the bathymetric affinities of extant species. Our results show that future studies are needed to better understand the evolutionary history and past distributions of this sawshark genus and their implications on current biogeographic patterns.

Keywords. Bahía Inglesa. Formation. South America. Elasmobranchii. Pristiophoridae.

Resumen. PRIMER REGISTRO FÓSIL DEL TIBURON SIERRA *PLIOTREMA* (PRISTIOPHORIDAE) PARA EL NEÓGENO DEL PACÍFICO SUDESTE (CHILE). Nosotros presentamos el primer registro fósil del tiburón sierra del género *Pliotrema* para el Pacifico sudeste. El material examinado fue obtenido de una localidad poco conocida llamada "Arenas de Caldera" en la región de Atacama en Chile. Los depósitos fosilíferos forman parte de la Formación Bahía Inglesa, la cual posee una edad probable de Mioceno medio a Plioceno temprano. No existen especies actuales de este tiburón sierra el Pacifico este, probablemente debido al establecimiento de las condiciones frías del Neógeno. El tipo de ambiente para los elasmobranquios reportados en este estudio es interpretado como demersal, basado en las afinidades batimétricas de las especies actuales. Nuestros resultados muestran que estudios futuros son necesarios para entender la historia evolutiva y distribución en el pasado de este tiburón sierra y las implicancias en sus patrones biogeográficos actuales.

Palabras clave. Formación Bahía Inglesa. América del sur. Chile. Elasmobranchii. Pristiophoridae.

SEVERAL CHONDRICHTHYAN TAXA have been reported from Neogene geological units along the Chilean coast up to now (*e.g.*, Suárez & Marquardt, 2003; Carrillo-Briceño *et al.*, 2013; Staig *et al.*, 2015; Villafaña & Rivadeneira, 2014, 2018; Partarrieu *et al*., 2018). Along the eastern Pacific coast of Chile, the Bahía Inglesa Formation (Fm.) is one of the well-known Neogene units where chondrichthyan and bony fish remains are abundant, with fossiliferous localities ranging from the middle Miocene to the Pliocene (Walsh, 2001; Villafaña *et al.*, 2019). Despite the large number of chondrichthyan remains recovered from the Bahía Inglesa Fm., as well as from other Neogene units of Chile throughout the 20th century, remains of the sawshark genus *Pliotrema* Regan, 1906 have not yet been reported. Villafaña and Rivadeneira (2014) were the first to mention the presence of *Pliotrema* fossils from the south-eastern Pacific (from the Atacama Region), but without providing figures or descriptions regarding these remains. The worldwide fossil record of *Pliotrema* is also scarce (Cappetta, 2012), and includes a few reports from the late Paleocene of California (Welton, 1974; not illustrated) and middle Miocene of South Africa (Case, 1973). Here, for the first time, we illustrate, describe and discuss the geological, paleobiogeographic and paleoecological implications of the presence of a fossil specimen of *Pliotrema*. The occurrence of *Pliotrema* in the Neogene of Chile fills an exceptional gap in the distributional and evolutionary history of this sawshark genus.

Institutional abbreviation. MPC, Museo Paleontológico de Caldera, Caldera, Chile.

Anatomical abbreviations. Bh, barbed hook; **Cap,** enameloid part of a rostral spine; **LSce**, less serrated cutting edge; **Pdl,** peduncle.

GEOLOGICAL SETTINGS

The Bahía Inglesa Formation (middle Miocene–lower Pleistocene) outcropping along the coastline of the Atacama region in Chile is characterized by a stratigraphic section

that correlates different units from the upper to lower coast, with oscillations in sea level combined with tectonics movements (Le Roux *et al*., 2016). Lithologically, it is represented by a domain of coquinoid sandstones, marls and mudstones. The mudstones include phosphorites, diatomites and volcanic ash layers (Rojo, 1985; Godoy *et al*., 2003). The fossiliferous locality "Arenas de Caldera", from where the fossil described here comes (MPC-217), is exposed in the community of Caldera, which forms part of an extensive emerged coastal platform. It extends 20 km in a NE-SW direction and contains at least six relicts of coastal terraces that are distributed from sea level to 230 m.a.s.l (Guicharrousse *et al*., 2018).

The Arenas de Caldera locality (Fig. 1; 27°4'37.62''S; 70°48'57.84''E) was mentioned in previous studies as being part of the Bahía Inglesa Fm. (Walsh & Suárez, 2005). This fossiliferous locality is mainly characterized by a sandstone sequence, where three well-defined stratigraphic horizons are distinguished (Fig. 2). Specimen MPC-217 was found in the second horizon, which is approximately 66 cm thick and represents a normal gradation that ranges from medium to very coarse sandstones with cross stratification.

Chronostratigraphy of the Bahía Inglesa Formation

According to Le Roux *et al.* (2016), the Bahía Inglesa Fm. ranges from the middle Miocene to Pleistocene. Although the Arenas de Caldera locality has not been unambiguously dated up to now, the presence of some fossil species can be used to infer a probable age range. In the eastern Pacific of South America, chondrichthyan taxa are commonly reported from Miocene to Pliocene sediments (Villafaña & Rivadeneira, 2014, 2018). For example, the extinct species †*Cosmopolitodus hastalis* is usually reported from Miocene sediments in Chile and Perú (Ehret *et al.*, 2012; Valenzuela-Toro *et al.*, 2016). Although the species *Carcharodon carcharias* is used as an indicator

of Pliocene age (de Muizon & Dvries, 1985), it also was reported as “probable” in late Miocene localities of Chile (Suárez & Marquardt, 2003; Walsh & Martill, 2006; Valenzuela-Toro *et al*., 2013). The only identified marine invertebrate from Arenas de Caldera locality layer is *Crassosstrea* sp., which is very abundant in sediments ranging from 15.3 to 4.2 Ma in the Bahía Inglesa Fm. (Le Roux *et al.,* 2016). Based on the stratigraphic position and biochron of some vertebrate and invertebrate taxa, this fossiliferous locality could be tentatively assigned to the middle Miocene to early Pliocene ages. Nevertheless, future radiometric dating could help to improve this inference.

MATERIAL AND METHODS

The single specimen MPC-217, which represents a rostral spine, is housed in the Museo Paleontológico de Caldera (MPC), Chile. The information about the current global distribution of *Pliotrema* species was obtained from Weigmann *et al.* (2020). Spine terminology follows Cappetta (2012), and the systematics for fossil and recent taxa are consistent with Weigmann *et al.* (2020) and Cappetta (2012).

According to Smith *et al*. (2015), the saw-teeth of sawfishes and sawsharks are not homologous to oral teeth, because they do not have the same origin (*i.e*., derived from dermal denticles). These modified dermal denticles are recently named as rostral spines in the description of a new species of sawshark (†*Pristiophorus laevis)* from the Eocene of Antarctica (Engelbrecht *et al*., 2017). We followed these recent studies and named our specimen MPC-217 as a rostral spine instead of rostral teeth.

157

158 **SYSTEMATIC PALEONTOLOGY**

159 Class CHONDRICHTHYES Huxley, 1880

160 Subclass ELASMOBRANCHII Bonaparte, 1838

161 Infraclass NEOSELACHII Compagno, 1977

162 Order PRISTIOPHORIFORMES Berg, 1958

163 Family PRISTIOPHORIDAE Bleeker, 1859

164 Genus ***Pliotrema*** Regan, 1906

165 **Type species.** *Pliotrema warreni* Regan 1906. Recent.

166 ***Pliotrema*** sp.

167 Figure 3. 1–3.6

168 **Material.** One rostral spine (MPC-217).

169 **Geographic distribution.** Arenas de Caldera locality.

170 **Stratigraphic distribution.** Middle Miocene–early Pliocene of Bahía Inglesa Fm.

171 **Description.** The rostral spine (MPC-217) is long, slender, and dorso-ventrally

172 flattened, reaching 42 mm in length and 16 mm in width (Fig. 3.1–3.4). The crown

173 (including the neck separating the crown from the peduncle) is slightly more than 4

174 times larger than the peduncle. The posterior cutting edge is weakly serrated with the

175 serrations restricted to the upper portion of the enameloid cap, but not reaching the apex

176 (Fig. 3.1–3.3). The anterior cutting edge is smooth and continuous and without any

177 serrations (Fig. 3.4). The anterior and posterior cutting edges are slightly tapered

178 laterally. The apex is acute and slightly bent towards the rear. The basal peduncle is

179 slender but broader than the crown jutting slightly out all around the crown in apical

180 view. It is subrectangularly shaped in its upper portion but with posteriorly elongated

181 base giving it an asymmetrical outline in dorsal and ventral views (Fig. 3.1–3.2). An

182 elliptically and deeply elongated foramen opens in the basal, concave face of the
183 peduncle (Fig. 3.5).
184 **Remarks.** Rostral spines of pristiophoriforms are readily distinguishable from those of
185 pristiform sawfishes in the development of a distinct peduncle, which is necessary to
186 anchor the spine to the lateral rostrum wall, whereas they are inserted deeply into
187 sockets in sawfishes lacking this peduncle (Wueringer *et al.*, 2009) The only other
188 known elasmobranch clade possessing rostral spines are extinct sclerorhnchoid
189 sawfishes, which, however, went extinct during the K/Pg boundary event (Kriwet &
190 Benton, 2004).
191 Pristiophoriform sawsharks include a single family, Pristiophoridae, to which
192 two extant genera (*Pliotrema* and *Pristiophorus*) and one extinct genus (†*Ikamanius*)
193 are assigned (Cappetta, 2012; Froese & Pauly, 2019). Although the extant and extinct
194 members of the family Pristiophoridae (†*Ikamauius, Pliotrema* and *Pristiophorus*)
195 display similar morphologies in their rostral spines (*i.e*., long and slender enameloid cap
196 with a basal peduncle), they can be easily distinguished (Cappetta, 2012; Weigmann *et*
197 *al.*, 2014). The rostral spines of extant *Pristiophorus* completely lack any serration
198 along the anterior or posterior cutting edge (Ebert & Cailliet, 2011; Ebert & Wilms,
199 2013; Engelbrecht *et al*., 2017; Villafaña *et al.*, 2019), whereas in †*Ikamauius*, the
200 anterior and posterior cutting edges are strongly serrated (Keyes, 1979; Cappetta, 2012).
201 The presence of posterior serrations on the rostral spine's cutting edges is a character
202 present in all known extant *Pliotrema* species; only varying in their degree and number
203 of serrations (Weigmann *et al.*, 2020; Fig. 4). Although the specimen MPC-217 from
204 the Bahía Inglesa Fm. displays the serrations along the posterior cutting edge as in
205 rostral spines of the genus *Pliotrema* (*i.e.*, posterior cutting edge), its posterior cutting-
206 edge serrations differ from those known from both fossil specimens (see Case, 1979;

Cappetta, 2012) and extant species (see Weigmann *et al.*, 2020) (Fig. 4). The comparison of fossil and extant specimens shows that the general spine morphology resembles that of *Pliotrema,* but that the serration of the posterior cutting edge is distinctly different. Following descriptions by Weigmann *et al.* (2020), two types of serrations are distinguished along the posterior cutting edge: type 1 consisting of a less serrated cutting edge and type 2 characterized by a serration developed into barbed hooks. Type 1 is similar to the reduced serration displayed by the fossil specimen reported here (Fig. 4.1), whereas type 2 is present in both fossil (Case, 1973; Cappetta, 2012) and extant specimens (Weigmann *et al.*, 2020) (Fig. 4.2–4.6). It nevertheless is mandatory that the fossil record of rostral pristiophoriform spines, especially those assigned to *Pliotrema* is revised to establish whether this kind of serration also occurs in other extinct members of this genus.

It is noteworthy that species level identification based on rostral teeth is not possible due to the high degree of morphological variation exhibited by *Pliotrema* species (Herman *et al.*, 1992; Weigmann *et al.*, 2020; Fig. 4) similar to what has been shown also for *Pristiophorus* (e.g., Engelbrecht *et al*., 2017). Consequently, it only is possible to assign specimen MPC-217 to the genus *Pliotrema*, but not to any species. Nevertheless, the single specimen is of utmost importance since it represents the first record of a fossil rostral spine that can be referred unambiguously to *Pliotrema* and thus adds to our knowledge about the diversity of Neogene elasmobranchs from the eastern Paleo-Pacific.

DISCUSSION AND CONCLUSIONS

Paleoenvironmental conditions

In the Arenas de Caldera locality, the horizon with the highest abundance of fossil remains (*i.e*., H2) (Tab. 1) exhibits a cross-stratification as the main sedimentary structure. Additionally, the inverse variation of the grain size, starting from medium to high coarseness, allows us to infer that this change occurred gradually. The sedimentary composition can be associated with off-shore coastal environments such as those described for the Bahía Inglesa Fm. at Playa Chorillos locality, as well as the area close to Los Dedos (Quezada *et al.*, 2007). The horizon "H2" concentrates the greatest variety of disarticulated and abraded vertebrate remains, with a high abundance of elasmobranch teeth (Tab. 1), and other vertebrates preliminarily identified as bony fishes, mammals (cetaceans, pinnipeds and sirenians), sea birds and reptiles (crocodylians). Invertebrates from the same layer include *Crassostrea* sp. and abundant indeterminate bivalves. The elasmobranch taxa identified in this layer have extant relatives with a maximum depth distribution of around 200 m (e.g., *Brachaelurus, Carcharias)* and 400 m (e.g., *Myliobatis*), respectively (Tab. 1). However, other sharks inhabiting continental and insular slopes (*e.g.*, *Carcharhinus*, *Odontaspis*, *Pristiophorus*) occur at depths of up to 1000 m depth (Tab. 1). In the case of *Pliotrema*, the three extant species are demersal sharks, but also show different depth preferences, from shallow to deep waters (Weigmann *et al*., 2020). *Pliotrema annae* Weigmann, Gon, Leeney & Temple, 2020 is associated with shallow waters (20–35m), *Pliotrema kajae* Weigmann, Gon, Leeney & Temple, 2020 with upper insular slopes and submarine ridges (214–320m), whereas *Pliotrema warreni* Regan, 1906 is a demersal species inhabiting the continental shelf and upper slope (10–915 m) (Weigmann *et al*., 2020). Nevertheless, according to Weigmann *et al.* (2020), the depth preferences of the two recently described species (*P. annae* and *P. kajae*) cannot be reliably inferred due to them being defined based on low numbers of known specimens. For instance, *P. annae*

255 possibly also occurs in deeper waters during the day but enters shallow water during the
256 night. Consequently, the mixture of depth distributions of the known elasmobranch taxa
257 reported from Arenas de Caldera locality and the unclear, but seemingly varied depth
258 preferences of the genus *Pliotrema* preclude a more elaborated interpretation. Thus, we
259 can only infer that the genus *Pliotrema* most likely inhabited a demersal environment
260 during the Neogene, based on the vertical distribution of extant representatives
261 (Weigmann *et al.*, 2020). Although, we represent here the first attempt to describe the
262 paleoenvironmental conditions of the Arenas de Caldera locality, more information
263 about its depositional conditions and associated fauna would allow a more accurate
264 conclusion.

265 **Paleobiogeographic implications**

266 *Pliotrema* is represented by three extant species: *P. warreni, P. kajae*, and *P. annae*,
267 with distributions in the southwestern Indian and southern Atlantic oceans (Weigmann
268 *et al.*, 2020) (see Fig. 5). The species *P. annae* is known from off the coast of Zanzibar,
269 *P. kajae* from off the coast of Madagascar and the Mascarene Ridge (Weigmann *et al*.,
270 2020), while *P. warreni* is known from the coast of South Africa and the coast of
271 southern Mozambique (Weigmann *et al*., 2020).

272 The oldest record of *Pliotrema* comes from the Paleocene of North America,
273 corresponding to isolated rostral spines (*Pliotrema* sp.) collected in the Lodo Formation,
274 a unit deposited in an outer sublittoral to upper bathyal environment with temperate
275 water conditions (Welton, 1974). Although there is no clear evidence, *Pliotrema* likely
276 could have migrated from North America to the southern region during the Neogene
277 (Fig. 5). At this time, the genus could have also migrated from the eastern Pacific
278 through the Central America Sea Way and proto-Caribbean to the Atlantic Ocean, and

279 then into the Western Indian Ocean. This hypothesis could be supported by the presence
280 of *Pliotrema* in the late Miocene of South Africa (Case, 1973). Today, extant species of
281 *Pliotrema* are absent along both eastern Pacific and western Atlantic coasts of the
282 Americas (Weigmann *et al.*, 2020). The extirpation of *Pliotrema* from both regions is
283 likely correlated with the climatic and oceanographic events that occurred in the last 20
284 Ma, especially those processes associated with the closure of the Central America Sea
285 Way (CAS) and the rise of the Panamanian Isthmus (see Carrillo-Briceño *et al.*, 2018),
286 the opening of the Drake passage (Scher & Martin, 2006), and the onset of cold coastal
287 upwelling cells of the Humboldt Current system (Dekens *et al.,* 2007). According to
288 Carrillo-Briceño *et al*. (2018), sharks were the most affected chondrichthyan group in
289 Tropical America, with at least 24 genera affected by extirpation/extinction processes.
290 The extirpation of the sawsharks (Pristiophoridae) from the eastern Pacific at the end of
291 the Neogene is also intriguing (Carrillo-Briceño *et al*., 2018). *Pristiophorus* had a wider
292 distribution in the eastern Pacific and western Atlantic oceans during Miocene and
293 Pliocene times (Carrillo-Briceño *et al*., 2016, appendix 1; 2018, table S3). However, the
294 only extant species inhabiting the continent (*Pristiophorus schroederi*) has a reduced
295 geographical distribution in the Bahamian region (between Cuba, Florida, and the
296 Bahamas) over continental and insular slopes between 400 and 1000 m (Kiraly, *et al.*,
297 2003; Nevatte & Williamson, 2020). According to Villafaña and Rivadeneira (2018),
298 the regional extirpation of chondrichthyan genera from the eastern Pacific of South
299 America (including Pristiophoridae) was caused by changes in salinity and sea surface
300 temperature. The limited thermal tolerance to cold-water conditions was suggested as
301 the main reason for the demise of Neogene sharks along the southeastern Pacific
302 (Partarrieu *et al.,* 2018). Still, other factors such as habitat loss due to sea level changes

(e.g., Cione *et al.*, 2007) also could have played an important role in structuring the Neogene elasmobranch associations along the American Pacific coast.

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FIGURE AND TABLE CAPTIONS

Figure 1. Location map of the Arenas de Caldera locality.

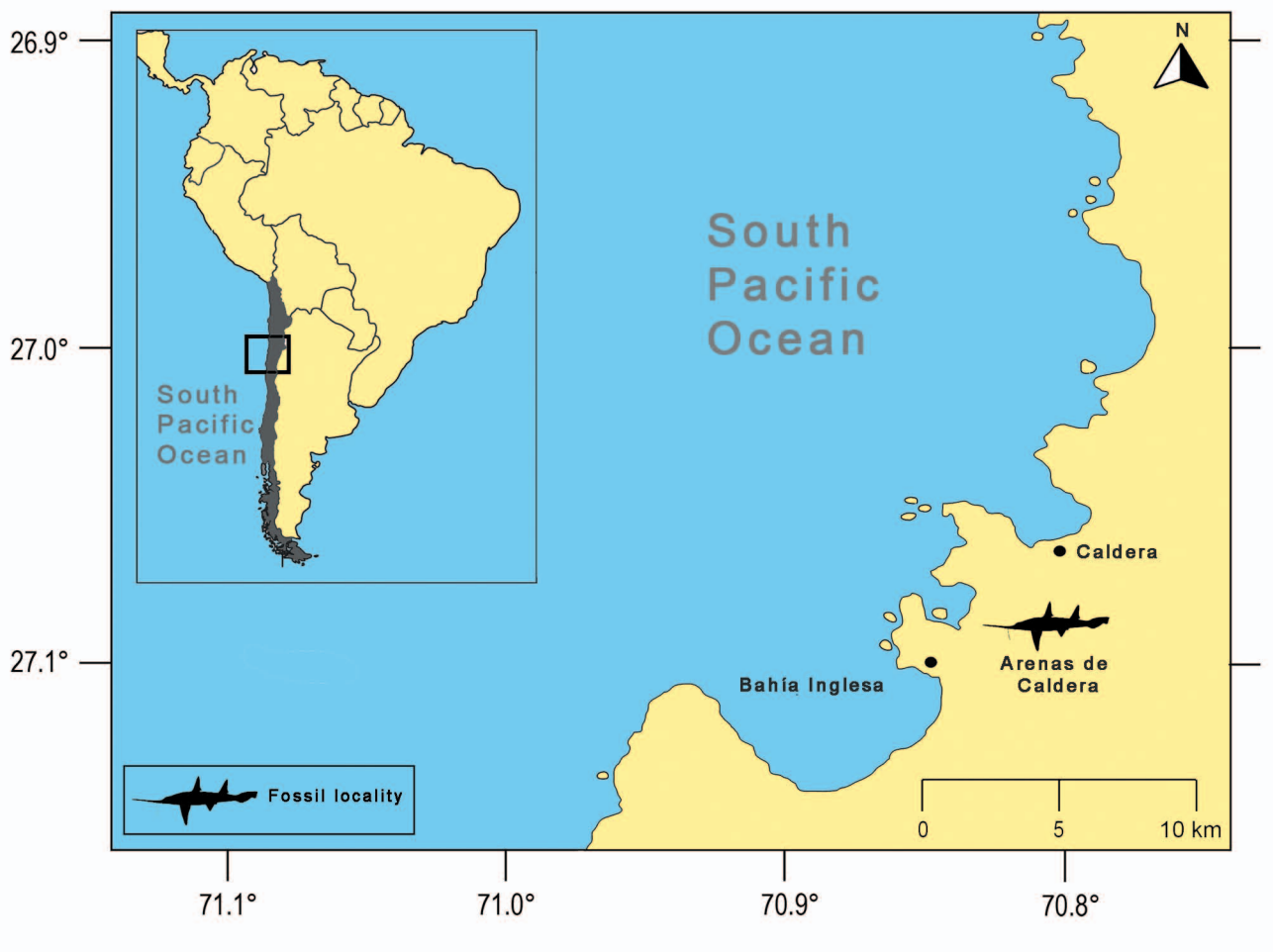
Figure 2. Stratigraphic section of the Arenas de Caldera locality.

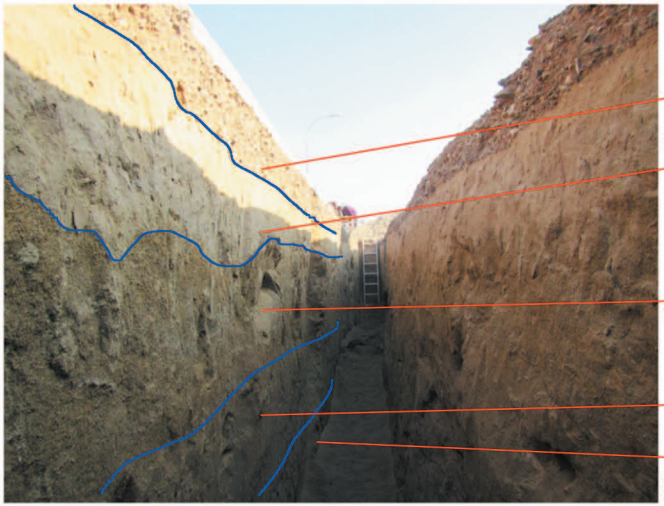
Figure 3. Rostral spine of *Pliotrema* sp. (MPC-127) from Arenas de Caldera locality. Views: **1**, ventral; **2**, dorsal; **3**, posterior; **4**, anterior; **5**, basal; and **6**, occlusal. Scale bar equals 1 cm.

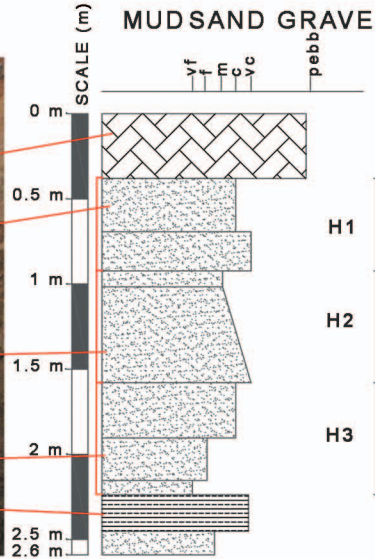
Figure 4. Line drawings of fossil and extant *Pliotrema* rostral teeth in dorsal views. **1**, this study (MPC-127); **2**, *Pliotrema* sp. from Miocene of South Africa (Cappetta, 2012); **3**, *Pliotrema* sp. from late Miocene of South Africa (Case, 1973); **4**, extant *Pliotrema annae* from Papa Unguja, Tanzania (Weigman *et al.*, 2020); **5**, extant *Pliotrema warreni* from Eastern Cape, South Africa (Weigman *et al.*, 2020); **6**, extant *Pliotrema kajae* from southwestern Madagascar (Weigman *et al.*, 2020). The specimens 2 and 3 were originally illustrated without scale. Bh, barbed hook; Cap, enameloid part of a rostral spine; LSce, less serrated cutting edge; Pdl, peduncle. Scale bar equals 5 mm.

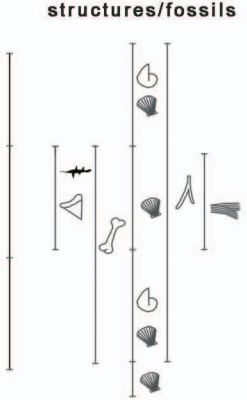
Figure 5. Map showing the geographic distribution of extant and fossil *Pliotrema*. Fossil distribution based on Case (1973), Welton (1974) and Cappetta (2012). Extant distribution based on Weigmann *et al.* (2020).

484 **Table 1.** Type of environment and depth distribution of the elasmobranch taxa reported
485 from Arenas de Caldera locality. Information taken from Fishbase (Froese & Pauly,
486 2019), Nevatte and Williamson (2020) and Weigmann *et al*. (2020).


26.9°
27.0°
27.1°
71.1°
71.0°
70.9°
70.8°
N
South
Pacific
Ocean
South
Pacific
Ocean
Caldera
Arenas de
Caldera
Bahía Inglesa
Fossil locality
0
5
10 km







Legend

Anthrophic filling

Poorly compacted sand

Coquina

Vertebrates

Elasmobranchs

Pliotrema sp.

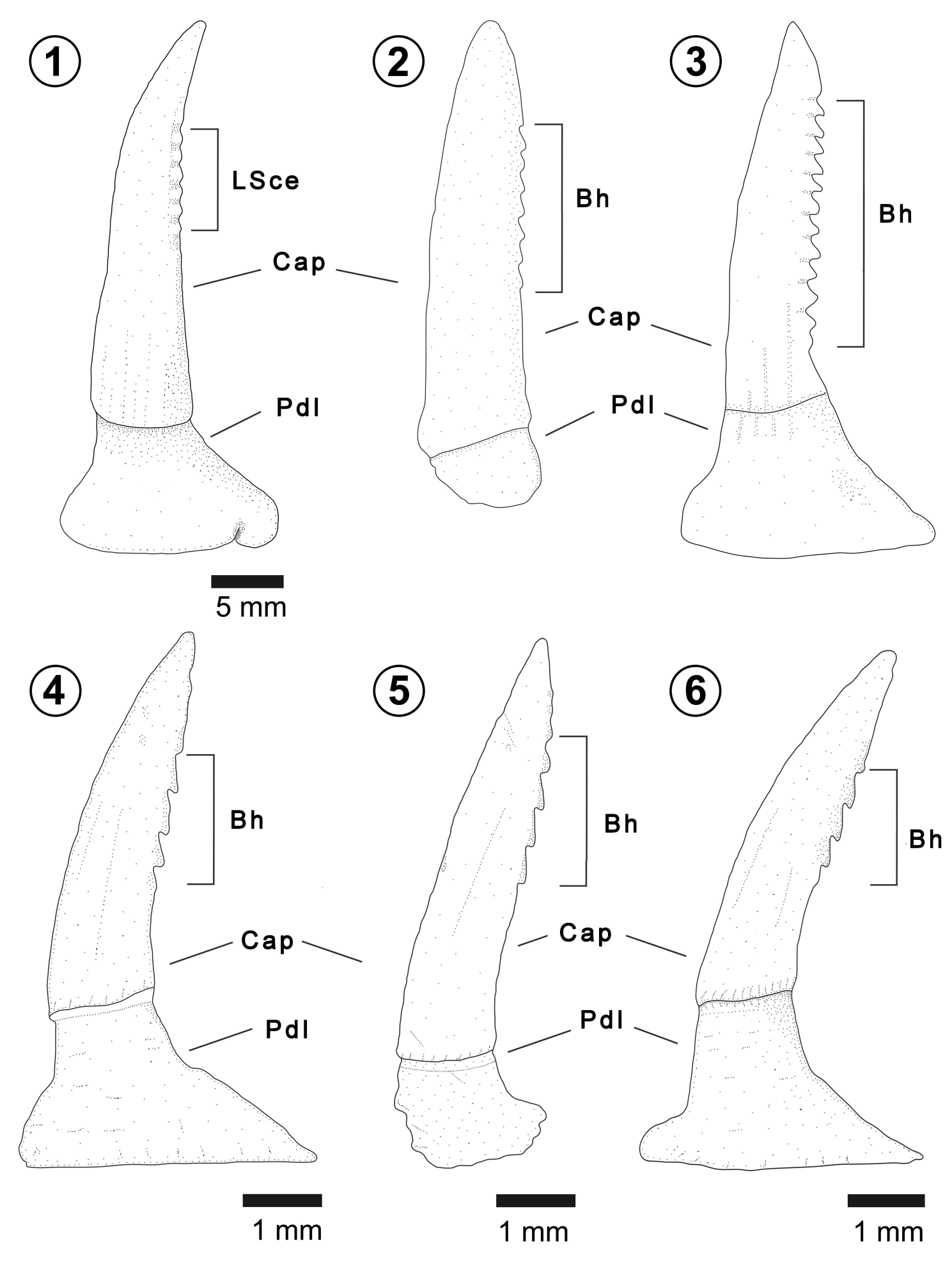
Gastropods

Bivalves

Bioturbation

Cross stratification


1
2
3
4
5
6


1
LSce
Cap
Pdl
5 mm
2
Bh
Cap
Pdl
3
Bh
4
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Cap
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1 mm
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1 mm
6
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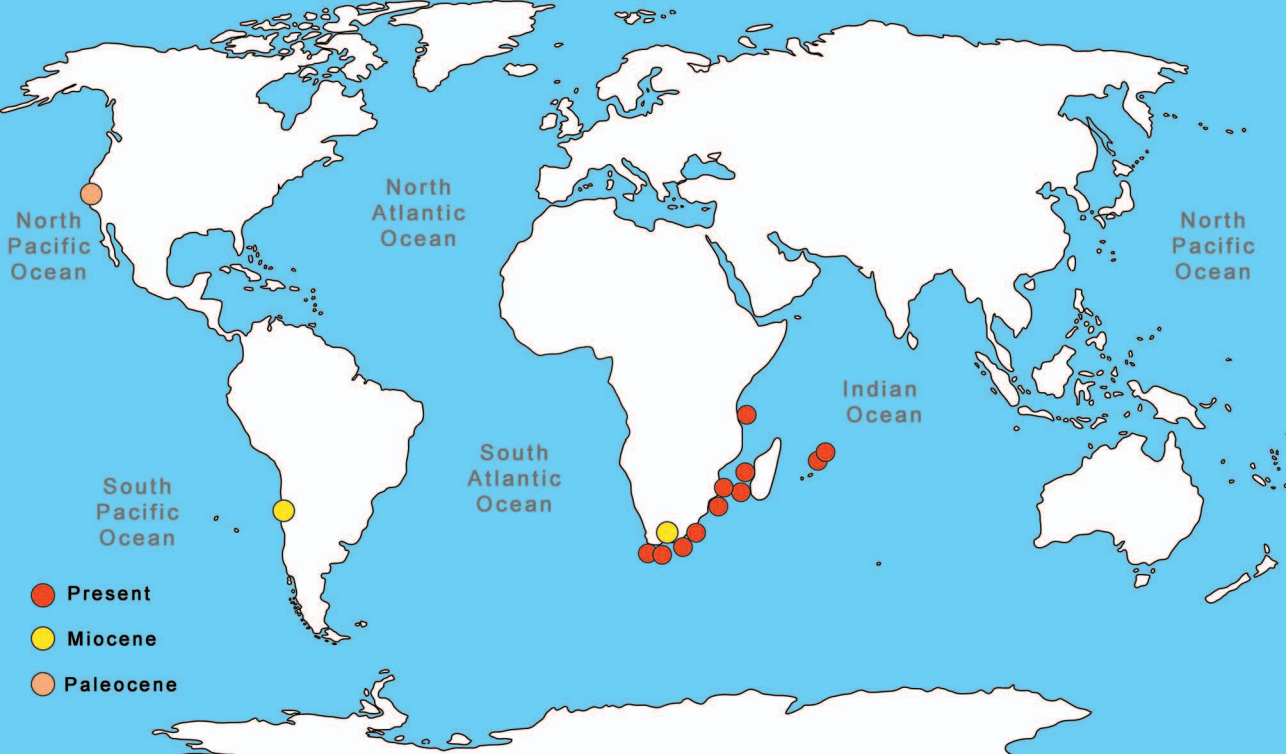
North Pacific Ocean
North Atlantic Ocean
North Pacific Ocean
Indian Ocean
South Atlantic Ocean
South Pacific Ocean
Present
Miocene
Paleocene

Table 1. Type of environment and depth distribution of the elasmobranch taxa reported from Arenas de Caldera locality. Information taken from Fishbase (Froese & Pauly, 2019), Nevatte and Williamson (2020) and Weigmann *et al.* (2020)

Order	Family	Fossil taxa	Environment	min depth (m)	max depth (m)
Orectolobiformes	Brachaeluridae	***Brachaelurus*** sp.	D-Ra	4	217
Carcharhiniformes	Carcharhinidae	***Carcharhinus*** sp.	D-Pn-Ra	0	1082
Lamniformes	Carcharhinidae	***Carcharias*** sp.	D-Ra	1	232
Lamniformes	Lamnidae	***Carcharodon carcharias***	Po	0	1200
Pristiophoriformes	Pristiophoridae	***Pliotrema*** sp.	D	10	430
Lamniformes	Lamnidae	†***Cosmopolitodus hastalis***	-	-	-
Lamniformes	Lamnidae	***Isurus*** sp.	Po	0	1752
Myliobatiformes	Myliobatidae	***Myliobatis*** sp.	Bp-D-Ra	0	422
Hexanchiformes	Hexanchidae	***Notorynchus*** sp.	B	0	570
Lamniformes	Odontaspididae	***Odontaspis*** sp.	Bp-Po	10	1015
Pristiophoriformes	Pristiophoridae	***Pristiophorus*** sp.	D-Po-Pn	0	1240

Bp, benthopelagic; D, demersal; Ra, reef-associated; Pn, pelagic-neritic; Po, pelagic-oceanic.